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The Effects of Volcanic Ash on Coniferous Foliage Physiology

THE EFFECTS OF VOLCANIC ASH ON CONIFEROUS FOLIAGE PHYSIOLOGY

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ABSTRACT

During the eruption of Mount St. Helens on May 18, 1980, varying amounts of ash were deposited from the volcanic plume on the coniferous ecosystems of Washington, Idaho and Montana. Almost 150 days later, needles of Douglas fir (*Pseudotsuga menziesii*) and Engelmann spruce (*Picea engelmanni*), growing at sites that received 1.0 cm or more of ash, still were heavily coated with 382 to 543 mg of ash/gram needle dry weight. Little variation in the amount of persistent ash on the needles of Douglas fir occurred over a distance of 220 km from the volcano. On the other hand, little ash persisted on the foliage of ponderosa pine (*Pinus ponderosa*) or white bark pine (*Pinus monticola*) growing at the same localities as the Douglas fir or Engelmann spruce. The needles of Douglas fir growing in areas which received less than 1.0 cm of ash also retained little or no ash. The surfaces of ash-laden needles of Douglas fir had significantly more epiphytic fungal colonies and hyphae associated with them than did needles with little or no ash. Needles of Engelmann spruce with heavy deposits of ash also had significantly more fungal colonies than did needles with less ash. The ash-laden needles created a new habitat to be exploited by the epiphytic fungi. The adherence of the ash particles to the mucilage produced by the fungal colonies and hyphae stabilized the ash layer so that it became a persistent feature on the surface of Douglas fir and Engelmann spruce needles. The ash had no apparent effect upon the internal anatomy of Douglas fir needles. Eight weeks after being artifically dusted with ash, needles had significantly less nonstructural carbohydrates than did needles from the control plants. Ash-coated and control seedlings had similar dark respiration rates, compensation points and light saturation levels. However, seedlings artificially coated with ash exhibited an enhanced photosynthetic rate.

The explosive eruption of Mount St. Helens on May 18, 1980 propelled a large ash plume into the atmosphere to an altitude of 20 to 25 km (Rosenfeld, 1980). By eight hours, the plume had reached an estimated volume of $2x10^6$ cubic km (Danielsen, 1981) and covered most of eastern Washington, northern Idaho and western Montana. An estimated 1.5 to 2.0 cubic km of ash fell on farm, range and forest lands (Hammond, 1980). The impact of ash on the agriculture of eastern Washington and northern Idaho has been adequately described by Cook et al. (1981). Except for a brief discussion in an article by del Moral (1980), the impact of volcanic ash on conifers has not been investigated.

MATERIALS AND METHODS--Branchlets were collected from various genera and species of conifers growing at 22 sites in Washington, Idaho and Montana on October 10 and 11, 1980. The amount of deposited ash and the location of the sampling sites are shown in Figure 1. The distance of the sites from Mount St. Helens, the elevation and the vegetation type at the sites are given in Table 1. Sites 1-7 were located in the Snoqualmie and Gifford Pinchot National Forests at a distance of 70 to 119 km from the volcano. Five of the sites (1, 2, 3, 5, 7) were located in areas that received moderate to heavy deposits of ash. Two sites (4 and 6) were exposed only to a light dusting of ash. All of seven sites had Douglas fir (*Pseudotsuga menziesii* Franco), and ponderosa pine (*Pinus ponderosa* Laws) grew at sites 3, 5, 6 and 7. Located at a higher elevation, site 2 had western hemlock (*Tsuga heterophylla* Sarg.), lodgepole pine (*Pinus contorta* Dougl.) and cascade fir (*Abies amabilis* Forbes). Since the distance from the volcano or elevation of the sites did not vary more than 32 km or 354 m respectively, sites 1 and 2 were compared to site 4 and sites 3, 5 and 7 were compared to site 6.

Sites 8 and 9 were located in a region of central Washington which received over 5.0 cm of uncompacted ash. Being a sagebrush steppe, this area is too arid to support stands of conifers. However, a few branchlets of Douglas fir, ponderosa pine and scotch pine (*Pinus sylvestris* L.) were collected from trees planted near an interstate highway rest stop and along a public right-of-way.

Ten sampling sites were located in the panhandle of Idaho. Five of these sites were in or adjacent to the Clearwater, St. Joe or Coeur d'Alene National Forests. Both Douglas fir and ponderosa pine grew at the similar sites 10, 11 and 12 (Table 1). However, sites 10 and 11 received a moderate to heavy deposit of ash while site 12 was subjected to a much lighter dusting. Ponderosa pine and Douglas fir grew at sites 13, 15, 18 and 19. Site 13 and 15 received moderate amounts of ash, and sites 18 and 19 were exposed only to a light dusting of ash. Engelmann spruce (*Picea engelmanni* Parry), western red cedar (*Thuja plicata* Donn), grand fir (*Abies grandis* (Dougl.) Lindl.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), white pine (*Pinus monticola* Dougl.), lodgepole pine and ponderosa pine grew at sites 14, 16 and 17. All these sites received heavy deposits of ash. Of the three sites in Montana, site 20 was at a high elevation of 1478 m. Engelmann spruce and lodgepole pine at this site were exposed to moderate amounts of ash. Ponderosa pine and Douglas fir at sites 21 and 22 received a relatively light dusting of ash.

The location of climatological stations is shown in Figure 1. Precipitation recorded at those stations from May 18 to October 10, 1980 is summarized in Table 2.

At all sites, branchlets were removed from trees 1.9 to 2.5 m above ground level. All sampled branchlets had been fully exposed to the ash fallout occurring on May 18, 1980. To reduce any possible roadside disturbance,

trees were sampled at some distance from the highway. The branchlets were placed directly into plastic bags with appropriate labels. Upon returning to the University of Montana, the samples were stored in a $4^{o}C$ refrigerator.

For a qualitative determination of the ash retained on the surface of needles, representative branchlets from the various sites were photographed on a copy stand. The central portion of the abaxial and adaxial surfaces of representative Douglas fir needles also were photographed at magnification of 15x using a dissecting microscope.

For scanning electron microscopic (SEM) studies, a central portion 1.0 cm long was removed from representative needles of Douglas fir, ponderosa pine, lodgepole pine and Engelmann spruce from various sites. Care was taken not to dislodge the ash deposits from the surface of the needles. The samples were first air dried and then dried at $50^{o}C$ for one hour before being affixed to studs and coated for examination with a Zeiss Novascan 30 scanning electron microscope. The more standard techniques of fixation and dehydration were not used, since they dislodged much of the ash. Both the abaxial and adaxial surfaces of the needles were examined with the SEM. The ash was intentionally dislodged from the surfaces of some fresh needles by washing them gently with a small paint brush. These needles then were oven dried at $90^{o}C$ for 12 hours before being examined with the SEM.

To determine the amount of persistent ash on the needles, twenty representative needles of Douglas fir or Engelmann spruce from each site were washed gently with a small paint brush. For dry weight determinations, the needles were oven dried at $90^{o}C$ for 12 hours. The washings from the needles were pulled through preweighed Millipore filters. The ash-laden filters were oven dried and weighed for the determination of the amount of persistent ash per gm of needle dry weight.

To investigate the extent of epiphytic fungi on the surface of needles, a 1.0 cm section was removed from the central portion of at least nine randomly selected two-year-old needles of Douglas fir and Engelmann spruce. When the adaxial surfaces of the sections were moistened, black fungal colonies became visible with a dissecting microscope at 8x magnification. When the colonies were too numerous to count with the dissecting microscope, the needle sections were photographed at a 5x magnification and number of colonies were determined from 35 mm negatives projected onto a piece of white paper.

To identify the dominant genera of epiphytic fungi, Douglas fir needles from sites 10 and 11 were rinsed ten times with sterile distilled water. Using sterile techniques, fungal colonies or pieces of hyphae were transferred to the surface of a two percent malt agar medium in small petri dishes. The fungi were incubated at 25^{o}C in continuous darkness. The fungi were periodically sub-cultured, and small portions of the cultures were removed for examination with the light microscope or were air dried for study with the SEM.

To determine the anatomical or morphogenetic effects of volcanic ash on Douglas fir needles, portions of needles were fixed in three percent gluteraldehyde buffered with 0.05 M potassium phosphate, pH6.8. The tissues were dehydrated in a graded ethanol series embedded in the medium of Feder and O'Brien (1968) and sectioned at 1-3 μm. Sections were stained with periodic acid-Schiff for carbohydrates (Feder and O'Brien, 1968) and with aniline blue black for proteins (Fisher, 1968).

To determine the effects of an artificial dusting of volcanic ash on carbohydrate accumulation, young seedlings of Douglas fir were obtained from the U.S. Forest Service on two different occasions. The first group of seedlings ranged in height from 7-12 cm, while the height of the second group was 18-19 cm. Randomly selected seedlings were randomly placed in a chamber

and coated with volcanic ash according to the modified methods of Atkins, Anderson and Tuft (1954). Randomly selected control seedlings also were subjected to the same conditions in the chamber as were the ash-coated plants but of course were not coated with ash. The amount of ash deposited on the foliage averaged 397 mg per gm needle dry weight, and the ash used to artificially coat the seedlings was collected in Missoula on May 18, 1980. The first group of seedlings were transferred to and maintained in the greenhouse of the Botany Department for three weeks. In order not to dislodge the ash from the foliage, plants were watered once a week with 30 ml from a plastic squeeze bottle. The second group of seedlings were placed in a growth chamber with 16 hours of light at an intensity of 30 $\mu E.m^{-2}.sec^{-1}$ for eight weeks and watered in a similar manner.

To determine the amount of nonstructural carbohydrates of needles, six plants each of ash-treated and control seedlings were clipped at midafternoon. The ash was washed from needles by agitating the stems and needles for one minute in 20 ml of distilled water. Needles were stripped from the stems, dried at $90^{o}C$ for 12 hr and ground to pass through a 60-mesh screen. The nonstructeral carbohydrates were quantified using the method of daSilveira et al. (1978). Since no large differences in carbohydrates were observed when ash-coated plants were compared to controls, and since ash-coated needles were difficult to section, carbohydrates were not qualitatively determined.

To investigate photosynthesis by artificially ashed and control seedlings, an open system gas exchange apparatus was utilized. Three seedlings of Douglas fir were sealed in a ventilated temperature controlled teflon-coated aluminum assimilation chamber with a glass top. A constant flow of air from a compressed air cylinder was passed through the chamber to a Beckman 215 infrared gas analyzer. Flow rates were maintained so that the CO_2 concentration in the

chamber did not drop below 300 µl. The difference between the CO_2 concentration of the compressed air and that of the air stream leaving the chamber was taken as the amount of CO_2 fixed by photosynthesis. Light was supplied by a General Electric Quartz lamp, and its photosynthetically active radiation was measured with a LiCor quantum meter. To measure light dependent photosynthesis, irradiance was decreased stepwise by covering the glass lid of the chamber with neutral density screens. The air temperature of the chamber was measured with a thermocouple and was held at 25°C for the various light intensities. Photosynthetic rates were expressed on a needle gram dry weight basis and represented an average of replicate samples of groups of three plants.

RESULTS--Sites Near Mount St. Helens--Douglas fir needles from sites located between the 1.0 and 3.0 cm ash isograms retained from 84 to 430 mg of ash/gm of needle dry weight (Fig. 2, 6). The ash coated both the abaxial and adaxial surfaces of the needles (Fig. 7, 8). All age classes of Douglas fir needles retained ash except at site 1 where the current year's needles had less ash than did older needles on the same branchlet. The ash also coated the older needles of the cascade fir and western hemlock growing at site 2. However, for the most part ponderosa pine or lodgepole pine needles from the four sites retained little or no ash (Fig. 9, 10). Needles from Douglas fir growing at the site (7) situated between the 0.25 and 1.0 cm ash isogram had only a small amount of ash (20 mg/gm needle dry weight). No ash was observed on the foliage of ponderosa pine at this site. When sites were subjected to 0.25 cm or less ash, little or no ash persisted on the needles of Douglas fir.

The needles of Douglas fir growing at site 1 had significantly more black epiphytic fungal colonies than did needles from site 4 (Fig. 3). There was no significant difference in the number of fungal colonies on Douglas fir needles

from sites 3 and 6 or from sites 5 and 7. However, the needles with persistent ash always had a larger number of hyaline hyphae growing among the tephra (Fig. 11). These needles also had significantly more black hyphae than did needles without persistent ash.

Central Washington Sites--The two central Washington sites (8, 9) received deposits of ash greater than 5.0 cm in depth. With scotch pine, the age of the needles made a significant difference in the amount of retained ash. The newer current year's needles had little ash while the older two-year-old foliage was heavily coated with ash. The Douglas fir needles retained 382 mg of ash/gm needle dry weight. Both surfaces of needles of all ages were encased in ash. Beneath the ash, the adaxial surface of the Douglas fir needles had only seven black fungal colonies. The foliage of ponderosa pine retained no visible ash.

Idaho Sites--The foliage of Douglas fir growing at sites 10 and 11 retained an average of 422 mg of ash/gm needle dry weight (Fig. 4). Both surfaces of needles of all ages were heavily encrusted with ash (Fig. 12, 13). However, foliage from Douglas fir trees growing at site 12 on the other side of the 1.0 cm ash isogram had only 15 mg of ash/gm needle weight (Fig. 12, 13). The needles of ponderosa pine growing at these three sites had no persistent ash.

The number of epiphytic fungal colonies growing beneath the ash on the surface of Douglas fir needles from sites 10 and 11 was significantly greater than those on foliage from site 12 (Fig. 5). At site 12, the fungal colonies were restricted to the adaxial groove of the needle, but at sites 10 and 11, the colonies were more evenly distributed on the adaxial surface of the heavily

ash-laden needles. Removal of the ash from the needles revealed large numbers of ash-coated fungal colonies and hyphae on the adaxial needle surface (Fig. 17). On the abaxial surface of the Douglas fir needles, conidia of *Cladosporium cladosporioides* (Fresen.) de Vries could be seen occasionally among the ash particles. When the ash was removed from the abaxial surface, a well-developed mycelial mat with multicellular conidia could be seen above the stomata (Fig. 18). At higher magnification, fibrils could be seen traversing the space between the hyphae and adjacent ash particles (Fig. 19). Ponderosa pine needles had no fungal colonies and only a small amount of hyphae.

Sites 13-17 were located at higher elevations (842-895m) than were sites 10-12. Douglas fir needles from sites 13 and 15 retained only a moderate amount of ash (44-54 mg/gm needle dry weight) but did have large numbers of epiphytic fungal colonies growing on their adaxial surfaces (Fig. 4, 5). The needles of ponderosa pine from the same sites had neither ash nor any significant numbers of epiphytic fungi.

Engelmann spruce, western red cedar, grant fir, subalpine fir, white bark pine and lodgepole pine grew at sites 14, 16 and 17. Regardless of age, all of the needles of Engelmann spruce were heavily coated with ash (94-540 mg of ash/gm needle dry weight) (Fig. 4). The older portions of the foliage of the firs and western red cedar also had some persistent ash deposits. There was no visible ash on the needles of the white bark pine. Only some of the older needles on the branchlets of lodgepole pine had ash; the current year's foliage lacked ash deposits.

All four surfaces of ash-laden Engelmann spruce needles had large numbers of epiphytic fungal colonies (Fig. 5, 21). Needles from sites 14 and 16 had more ash and significantly more colonies than did needles from site 17. The

older needles of grand fir and lodgepole pine also had numerous fungal colonies.

The foliage from Douglas fir growing at sites 18 and 19 retained no ash and had few epiphytic colonies (Fig. 4, 5). .

Montana Sites--Site 20 was a high elevation Engelmann spruce/lodgepole pine site. The needles of the spruce retained 77 mg of ash/gm needle dry weight and had a very large number of fungal colonies (Fig. 4, 5). The foliage of the lodgepole pine was also heavily coated with ash and had numerous fungal colonies.

Sites 21 and 22 received from 0.15 to 1.0 cm of ash. The Douglas fir foliage had no persistent ash and only a few epiphytic fungal colonies in the adaxial groove of the needle.

The dominant genera of epiphytic fungi growing on the adaxial surface of needles of Douglas fir at sites 10 and 11 were *Hormonema dermatioides* (Lund and Melin) and an unidentified *Loculoascomycete* with numerous blastoconidia. On the abaxial needle surface, the dominant genera were *Monodictys* and *Leptographium*.

The volcanic ash had no anatomical or morphogenetic effects upon Douglas fir needles. The internal anatomy of needles coated with ash did not differ from that of control needles.

After three weeks in the greenhouse, the amount of nonstructural carbohydrates of needles from artificially ash-coated seedlings did not differ significantly from the carbohydrates of needles from control plants (Table 3). However, there was a certain trend toward a decrease in nonstructural carbohydrate in the ash-coated needles. When seedlings were maintained in a growth chamber for eight weeks, needles artificially coated with ash exhibited

a significant decrease in the amount of nonstructural carbohydrate when compared to the control.

When photosynthesis of artificially ashed seedlings was compared to that of control plants, it was found that the two groups of seedlings exhibited similar dark respiration rates, compensation points and light saturation levels (Fig. 22). However, seedlings coated with volcanic ash did fix CO_2 at a faster rate than did the control seedlings.

DISCUSSION--On May 18, 1980, large amounts of ash from the explosive eruption of Mount St. Helens descended upon the diverse forest ecosystems of Washington, Idaho and Montana. Almost 150 days later, the needles of Douglas fir and Engelmann spruce growing at locations which received at least 1.0 cm of ash were still heavily coated with volcanic ash. To a slightly lesser extent, western red cedar, cascade fir, grand fir and subalpine fir needles also had persistent ash deposits. Even though the physical characteristics of the tephra did vary with distance from the volcano (Fruchter et al., 1980), the amount of ash retained by Douglas fir foliage failed to do so. Needles from trees growing as close as 113 km and as far as 434 km from the volcano were coated with as much as 430 to 440 mg of ash per gm of needle dry weight. Foliage from sites receiving 1.0 to 3.0 cm of ash actually retained more ash than did needles of trees growing at a location receiving over 5.0 cm of tephra. The greatest amount of ash retained by any conifer foliage (540 mg/gm needle dry weight) was observed on the needles of Engelmann spruce growing at a site 456 km from Mount St. Helens.

In stark contrast to the ash-laden foliage of Douglas fir and Engelmann spruce, the needles of ponderosa pine and white bark pine growing at the same

location retained little or no ash. As might be expected, the needles of Douglas fir growing at sites which received less than 1.0 cm of ash also had little or no ash.

The persistence of ash on the foliage of Douglas fir and Engelmann spruce could not be explained by the climatology of the region (Table 2). All locations with ash-coated needles received a total of 6.86 to 28.37 cm of precipitation during the 150-day period after the eruption of the volcano. This amount of precipitation should have dislodged the ash from the surface of the needles. However, closer examination of the climatological data revealed that all sites except one received only gentle rainfall, which presumably could not dislodge the ash effectively. In fact, the gentle rainfall may have caused some redistribution of ash from the adaxial to the abaxial surface of the needle.

The retention of ash by Douglas fir and not the neighboring ponderosa pine was most intriguing. The many horizontal needles of Douglas fir could support more ash deposition than the vertical needles of ponderosa. Some of the ash may have adhered initially to the gelatinous epiphytic fungi growing in the midrib groove and near the stomata of the Douglas fir needle. Since the fungi occupy only a small portion of the needle surface (Carroll, 1979), it was highly unlikely that there were enough mucilaginous fungi on the needle surfaces to account for the initial retention of large amounts of ash. In fact, needles of trees growing in Central Washington retained large amounts of ash but had only a few epiphytic colonies. In all likelihood, the ash initially interacted with and adhered to the cuticle of Douglas fir needles in a different manner than it did with the needles of ponderosa pine. When young epiphytic-free seedlings of Douglas fir were artificially dusted with volcanic ash, not all of the ash could be dislodged by simply washing

the needles with running water (S. Marvel, Pers. Commun.).

Needles of scotch pine and the true firs exhibited an age-dependent retention of ash. The younger, current year's needles had significantly less ash than did the older needles. In all likelihood, the younger needles were still enclosed within the buds or had just begun to expand when the ash fell. The smaller amounts of ash on the surface of the younger needles presumably resulted from secondary deposition by wind.

Even though the ash initially clung to the surfaces of crop plants, most of the ash was eventually shed from the leaf surfaces (Cook et al, 1981). With conifers, del Moral (1981) reported that western red cedar growing just a few km from the blast zone retained ash more tenaciously than did Douglas fir. His observations seemingly contradict those made during this investigation. Perhaps, the physical nature of the ash near the volcano was very different than that deposited further away.

The ash-laden needles of Douglas fir growing on the eastern slope of the Cascade Mountains had significantly more black hyphae on their surfaces than did needles without persistent ash. These hyphae as well as hyaline hyphae penetrated the ash layer and frequently were observed growing among the ash particles.

Large numbers of black epiphytic colonies of *Hormonema* and other fungi grew under the ash on the adaxial surface of Douglas fir needles from the Idaho sites. Needles with little or no ash had significantly fewer epiphytic colonies. With Engelmann spruce, epiphytic fungal colonies could be found on all four surfaces of the needles, and needles with less ash had significantly fewer epiphytic colonies than did needles with large amounts of ash.

Cells of *Hormonema* are embedded in an extracellular gelatinous matrix. In the absence of ash, these epiphytic colonies are primarily restricted to the midrib depression on the adaxial surface of Douglas fir needles (Bernstein and Carroll, 1977; Carroll, 1979). Colonies presumably are not found on the lamina of needles because this surface has fewer establishment sites and a harsher microclimate (Bernstein and Carroll, 1977). When ash was deposited on the needle surface, the microhabitat and climate was quickly altered. The ash could hold moisture for a longer period than the naked needle and contained many micronutrients (Fruchter et al., 1981) which were available to the fungi for growth. The small number of colonies in the midrib groove extended over the uncolonized needle surface and formed new colonies. These colonies in turn produced more new colonies. As a result, the fungal colonies became distributed over the entire adaxial surface of the ash-laden needle. Since ash adheres to the gelatinous slime of the colonies, more and more ash became stabilized on the surface of the needle. The growth of hyphae of other epiphytic fungi among the tephra further stabilized the ash layer on the needle.

Since the abaxial surface of Douglas fir needles have more establishment sites and a more moderate microclimate, more epiphytic fungal colonies are normally found on that surface than on the adaxial one (Bernstein and Carroll, 1977; Carroll, 1979). With ash-laden needles, the abaxial fungi existed not as individual colonies but as a continuous mat of hyphae over the stomatal surface.

Ash deposits have been shown to have altered the habitats of other fungi (Cook et al., 1981). The moist ash layer on the soil persumably provided ideal conditions for the germination, growth and fruiting of the pathogenic fungi, *Sclerotinia*, *Phoma* and *Cercosporella*.

The exploitation of the new ash habitat by epiphytic fungi may have had profound effects on conifer productivity. Phyllosphere fungi derive their carbon from leaf surfaces. In fact, certain surface yeasts have been shown to utilize the cuticular waxes of needles (McBride, 1972). The persistent ash layer may have reduced light intensities and interfered with photosynthetic gas exchange. Reduced photosynthetic capabilities and the removal of carbon by the epiphytic fungi may have stressed and weakened the needles to such a degree as to affect the future production of wood, cones and new needles.

Nonstructural carbohydrates of needles were significantly reduced eight weeks after Douglas fir seedlings were artificially coated with volcanic ash. Presumably, the ash on the surface of the needles affected photosynthesis by reducing light intensities or CO_2 concentration by altering stomatal function. However, photosynthetic rates of ash-coated seedlings actually were greater than those of the control plants. Dark respiration rates, compensation points and light saturation levels were similar for both the ash-coated and control seedlings.

In order to measure photosynthesis, the seedlings are placed in a closed system through which air is circulated. Once enclosed in such a chamber, plants will increase the internal humidity by transpiring water vapor. Since the thin layer of ash on the needle is hygroscopic, water more likely would be retained for a longer time at the needle surface before it is lost to the air stream passing through the chamber. A relatively higher humidity would be expected to cause the guard cells to increase the stomatal aperature. This change in turn would allow for the enhanced uptake of CO_2 into the needle. Since CO_2 in the needle would no longer be limiting, photosynthesis could proceed at an enhanced rate.

In nature, the stomatal surface of Douglas fir needles was coated with thick layers of ash and fungi which actually may have reduced light intensities and acted as a barrier against the diffusion of CO_2 required for photosynthesis. In a more open windier system, water vapor would be expected to evaporate more readily from the ash, resulting in the closure of stomata and a reduction in the amount of CO_2 fixed during photosynthesis.

TABLE 1

The Distance from Mount St. Helens, Elevation and Vegetation Type of Sampling Sites

Site	Distance From Mt. St. Helens-km	Elevation -m	Vegetation Type[1]
1	70	682.8	Fir-Hemlock
2	86	1268.0	Fir-Hemlock
3	102	737.6	Western Ponderosa
4	102	1036.3	Fir-Hemlock
5	113	591.3	Western Ponderosa
6	114	877.8	Western Ponderosa
7	119	609.6	Western Ponderosa
8	272	396.2	Sagebrush Steepe
9	305	554.7	Sagebrush Steepe
10	426	787.0	Douglas Fir
11	434	658.4	Douglas Fir
12	435	662.0	Douglas Fir
13	435	865.6	Western Ponderosa
14	454	853.4	Cedar-Hemlock-Pine
15	456	877.8	Cedar-Hemlock-Pine
16	456	894.6	Cedar-Hemlock-Pine
17	460	841.6	Cedar-Hemlock-Pine
18	460	359.7	Western Ponderosa
19	498	426.7	Western Ponderosa
20	523	1477.6	Western Spruce-Fir
21	580	853.4	Western Ponderosa
22	644	1073.8	Western Ponderosa

[1]after Küchler (1964)

TABLE 2

United States Department of Commerce Precipitation
Data for the Period May 18 to October 10, 1980

Location	Total Precipitation -cm	Number of Days >0.25cm	>1.27cm	>2.54cm
Washington				
a. Packwood	17.30	19	4	0
b. Yakima	6.76	8	0	0
c. Ritzville	10.85	11	3	0
d. Spokane	11.20	10	2	0
Idaho				
e. Cour d' Alene	20.93	19	7	0
f. Tensed	17.55	17	5	0
g. St. Maries	24.31	12	7	4
h. Elk River	28.37	29	5	0
Montana				
i. Haugan	31.14	27	9	2
j. Superior	23.75	27	4	2
k. Missoula	22.58	21	3	2

TABLE 3

The amount of nonstructural carbohydrates as glucose equivalents in artificially ash-coated and control seedlings of Douglas fir after three and eight weeks of treatment.

Treatment	Mg glucose/mg needle dry weight
Three weeks	
Control needles	0.053 ± 0.009[1]
Ash-coated needles	0.043 ± 0.005
Eight weeks	
Control needles	0.039 ± 0.003
Ash-coated needles	0.026 ± 0.004

[1]95 percent confidence limits

Fig. 1. Depth of volcanic ash in cm, (●) location of sampling sites (see Table 1) and (△) location of selected climatological sites (see Table 2). Map adapted from Cook et al. (1981).

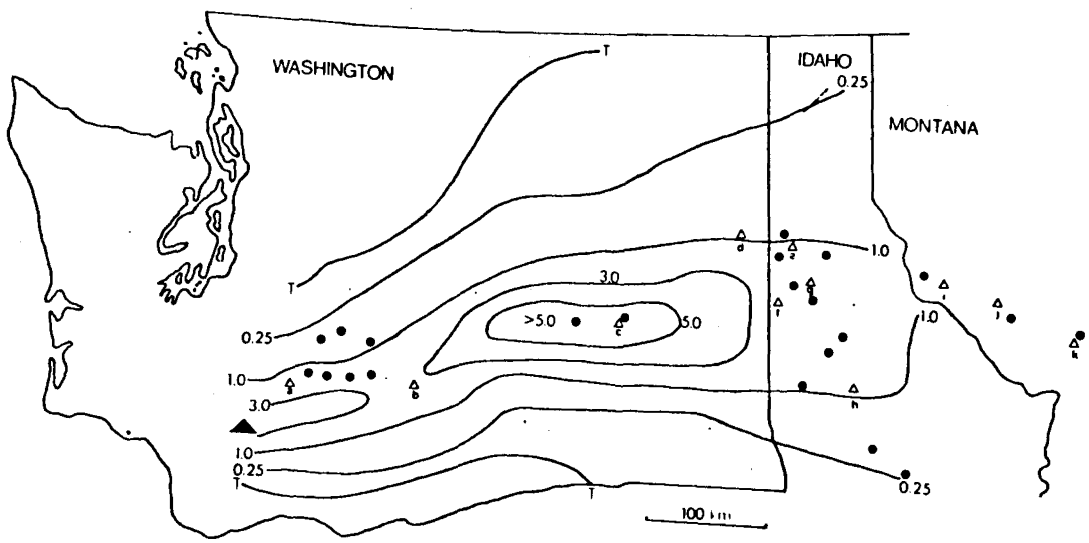

WASHINGTON
IDAHO
MONTANA
T
0.25
1.0
3.0
>5.0
5.0
100 km

Fig. 2. Depth of volcanic ash in cm and histograms representing the amount of ash retained by Douglas fir needles. Each unit on a histogram represents 100 mg of ash/gm of needle dry weight. Map adapted from Findley (1981).

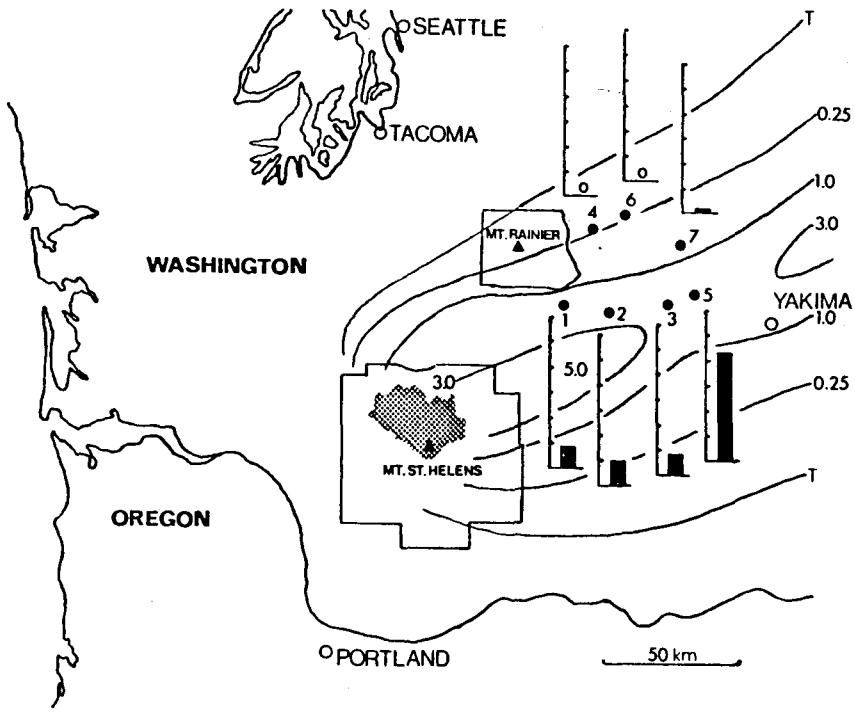

SEATTLE
TACOMA
WASHINGTON
OREGON
PORTLAND
MT. RAINIER
MT. ST. HELENS
YAKIMA
T
0.25
1.0
3.0
5.0
1
2
3
4
5
6
7
50 km

Fig. 3. Depth of volcanic ash in cm and histograms representing the number of black epiphytic fungal colonies growing on the adaxial surface of Douglas fir needles. Each unit on a histogram represents 10 colonies. Map adapted from Findley (1981).

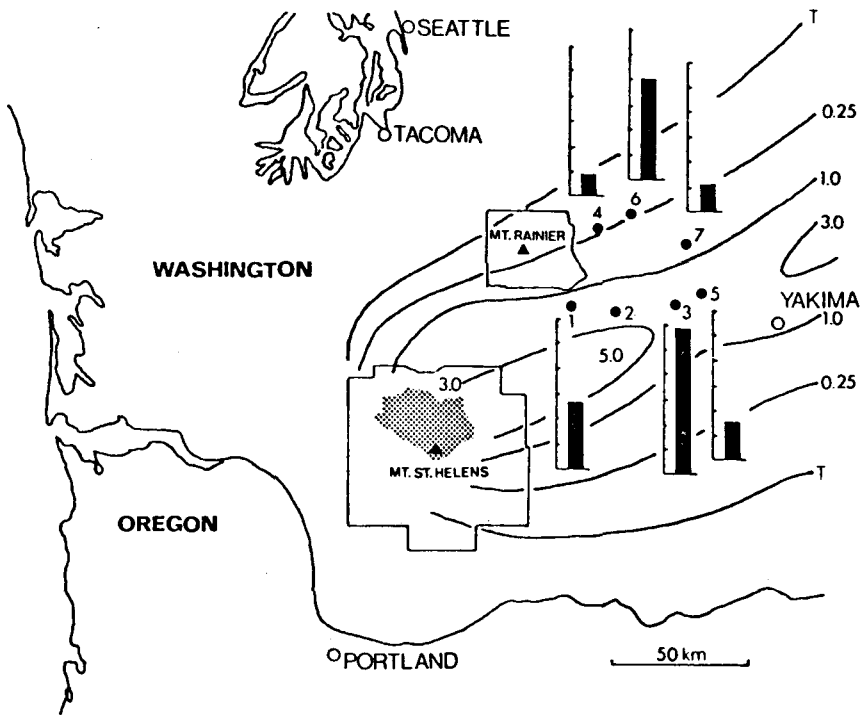

SEATTLE
TACOMA
WASHINGTON
OREGON
PORTLAND
MT. RAINIER
MT. ST. HELENS
YAKIMA
T
0.25
1.0
3.0
5.0
1
2
3
4
5
6
7
50 km

Fig. 4. Depth of volcanic ash in cm and histograms representing the amount of ash retained by Douglas fir and Engelmann spruce needles (s). Each unit on a histogram represents 100 mg of ash/gm of needle dry weight. Ash depth taken from Cook et al. (1981).

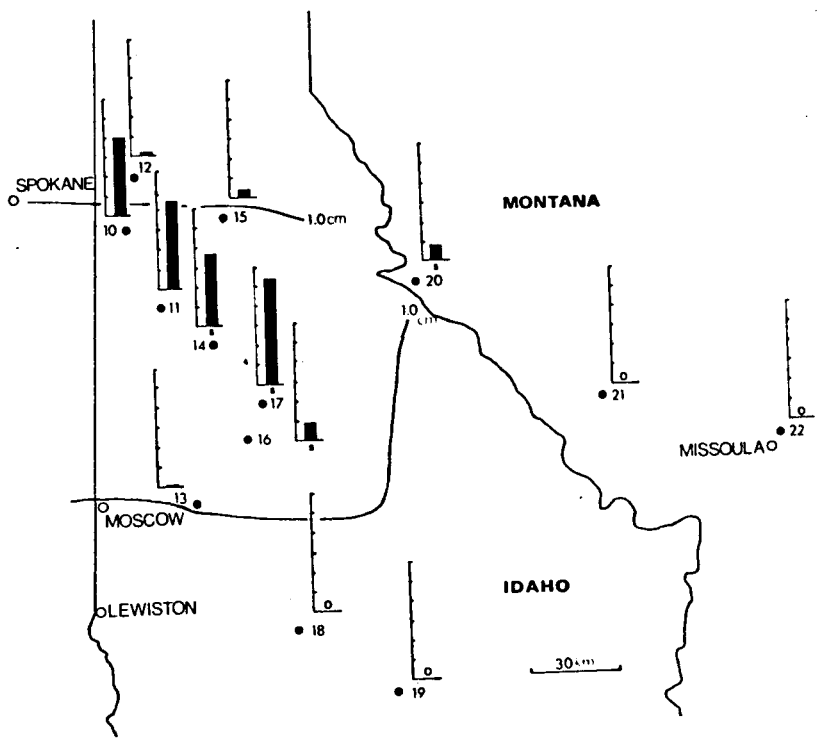

SPOKANE
MOSCOW
LEWISTON
MISSOULA
MONTANA
IDAHO
1.0cm
1.0 cm
30 km
10
11
12
13
14
15
16
17
18
19
20
21
22

Fig. 5. Depth of volcanic ash in cm and histograms representing the number of black epiphytic fungal colonies growing on the adaxial surface of Douglas fir needles and on one of the four surfaces of Engelmann spruce needles (s). Each unit on a histogram represents 100 colonies. Ash depth taken from Cook et al. (1981).

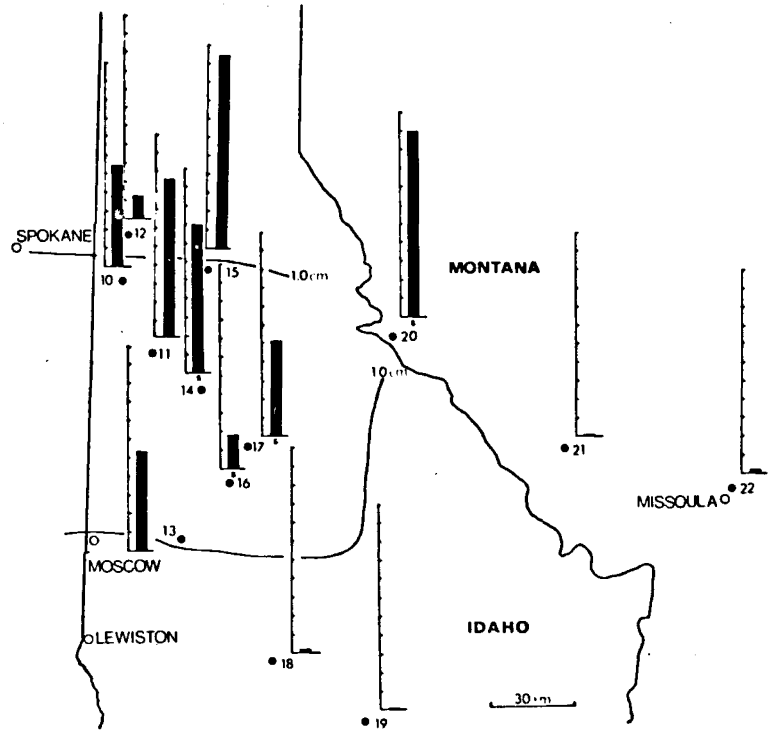
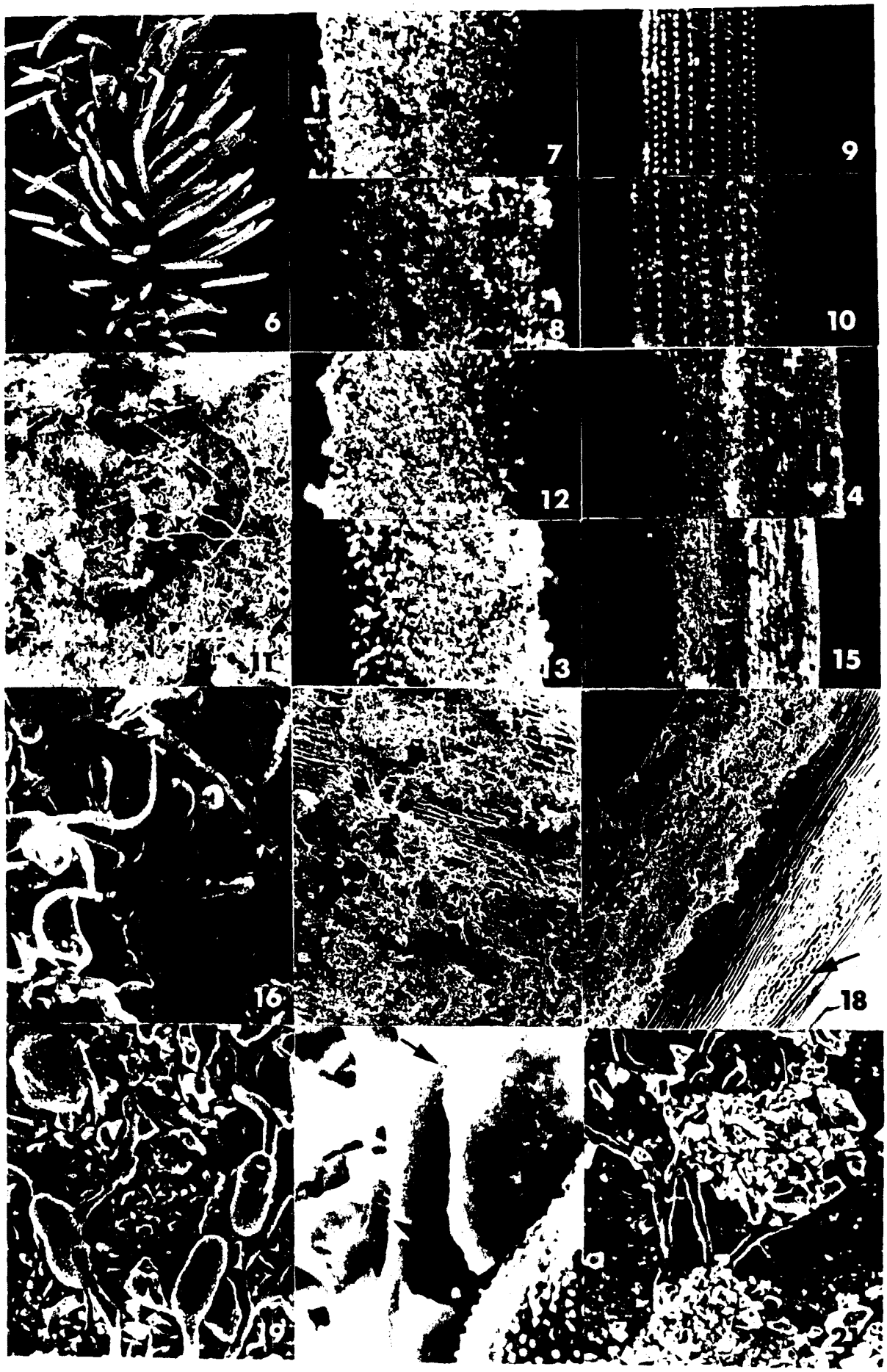

SPOKANE
MOSCOW
LEWISTON
MONTANA
IDAHO
MISSOULA
10
11
12
13
14
15
16
17
18
19
20
21
22
1.0 cm
1.0 cm
30 km

Fig. 6-21. 6. A portion of a Douglas fir branchlet from sampling site 5 showing ash deposits on the needles x 1. 7. Adaxial surface of a needle of Douglas fir needle from site 5 showing ash deposition x 25. 8. An ash-laden abaxial surface of a needle of Douglas fir needle from site 5. x 25. 9. Adaxial surface of a needle of ponderosa pine from site 5. A small amount of ash is visible between the stomatal bands. x 25. 10. Abaxial surface of needle of ponderosa pine from site 5. x 25. 11. SEM view of fungal hyphae among the ash particles on a Douglas fir needle from site 5. x 127. 12. Adaxial surface of an ash-laden needle of Douglas fir from site 10. x 25. 13. Abaxial surface of a needle of Douglas fir from site 10. x 25. 14. Adaxial surface of a Douglas fir needle from site 12. x 25. 15. Abaxial surface of a needle of Douglas fir from site 12. x 25. 16. SEM view of *Cladosporium* conidia and hyphae in the ash layer on the abaxial surface of a Douglas fir needle from site 11. x 950. 17. SEM view of the adaxial surface of a Douglas fir needle from site 10 with the ash removed showing numerous fungal colonies and hyphae. x 75. 18. SEM view of the abaxial surface of a Douglas fir needle from site 10 with the ash removed showing the hyphal mat over the stomata (arrow). x 43. 19. SEM view of conidia associated with the hyphae on the abaxial surface of a Douglas fir needle from site 10. x 790. 20. SEM view of a fungal hypha attached to ash particles by fine fibrils (arrows). Abaxial surface of a Douglas fir needle from site 10. x 3500. 21. SEM view of ash coated fungal colonies on the surface of a Engelmann spruce needle from site 14. The ash has been removed. x 560.

Fig. 22. Photosynthesis of seedlings eight weeks after being artificially coated with volcanic ash▲and control seedlings△.


6
7
8
9
10
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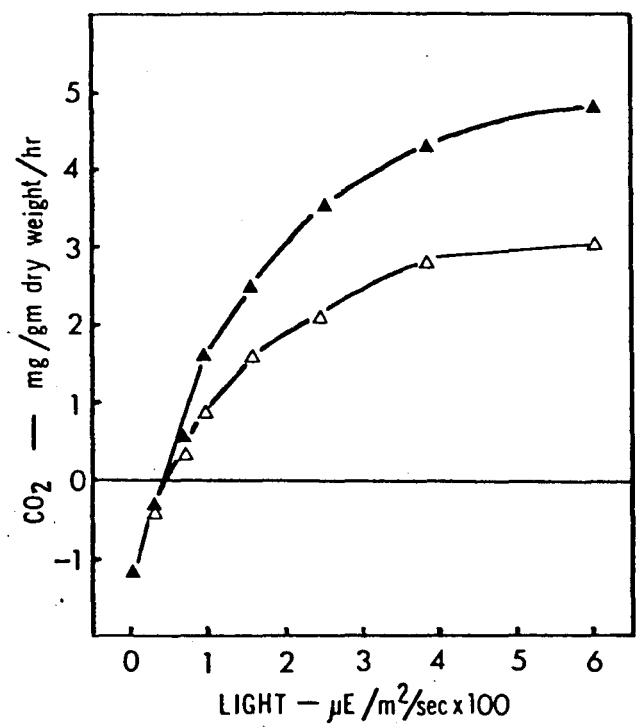
21


5
4
3
2
1
0
-1
CO_2 — mg/gm dry weight/hr
0
1
2
3
4
5
6
LIGHT — μE/m^2/sec x 100

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